NOTES ON FEEDING AND DIGESTION IN PTEROCERA AND VERMETUS, WITH A DISCUSSION ON THE OCCURRENCE OF THE CRYSTALLINE STYLE IN THE GASTROPODA

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.)

Late Balfour Student in the University of Cambridge; Physiologist at the Plymouth Laboratory

WITH SIX TEXT-FIGURES

CONTENTS

1. INTRODUCTION.

OF the population of coral reefs, the Mollusca are second only in importance to the Coelenterata. In the work of the Expedition more attention was therefore paid to molluscs than to any other animals apart from corals. The breeding, growth and habits of *Trochus niloticus* were studied by Mr. F. W. Moorhouse (see Vol. III, No. 5), and of *Pinctada margaritifera* by Mr. A. G. Nicholls (1931), while the breeding of the chiton, *Acanthozostera gemmata*, and of the clam, *Hippopus hippopus*, formed a portion of the investigations on the breeding habits of reef animals undertaken by the Shore Party, the results of which will be published in Volume III of these reports. It was natural that such limited time as could be spared from the extensive programme of work on the physiology of corals

should be devoted to work on the feeding and digestion of reef molluscs. The greater part of these investigations were concerned with the Tridacnidae, which are of especial interest owing to their possession of zooxanthellae. This work will form the subject of a later paper in this volume. Research was also undertaken on the common reef gastropod, *Pterocera crocata*, and on the very large *Vermetus*, found only on the outer barrier reefs, and which is also of interest owing to the uncertainty which has previously existed as to the mode of feeding in this genus.

Work on these two gastropods forms the subject of this paper. Both of these animals possess large crystalline styles, and the opportunity has been taken to discuss the occurrence of this remarkable organ in the Gastropoda, and correlate it with the feeding habits and food of those gastropods which possess it.

2. PTEROCERA CROCATA.

(a) OCCURRENCE AND HABITS.

The spider shells, of which *Pterocera crocata* is the commonest species, are amongst the most abundant, and are certainly, on account of their size, the most striking of reef gastropods. Stephenson, Stephenson, Tandy and Spender, in their account of the ecology of Low Isles and other reefs (Vol. III, No. 2), have pointed out that this species is a characteristic member of the fauna of the reef flat and mangrove park at Low Isles, and that a species of *Pterocera* was also abundant on Yonge Reef, one of the Outer Barrier reefs. My own observations showed that it was abundant everywhere, from the Torres Strait in the north to the Capricorn Group at the south. It occurs always on the surface of reefs, never on the sides or at the bottom, and, for reasons which will be apparent when its feeding habits are discussed, always in sandy depressions between coral heads or on sandy expanses in the lee of reefs, or associated with mangrove formations, such as that at Low Isles. It never burrows into the sand, but lies freely exposed, occasionally out of water at low tide, but usually covered with water in shallow pools. The shell, with the six projections which are responsible for its common name, is too well known to need description. It attains a length, including the spines, of about 18 or 20 cm. The powerful foot is armed with a long, very sharp operculum, and the animal progresses by a series of sudden movements, digging the operculum into the sand and then extending the foot. The creeping sole, characteristic of so many gastropods, has been lost, and the animal could not move freely except on a sandy bottom. The foot can be protruded for a great distance. If an individual is turned over, the foot is extended so far that the operculum is hooked under the shell where it rests on the ground. Then, by a convulsive movement, the animal rights itself.

The Strombidae, to which *Pterocera* belongs, are apparently all adapted for life on the surface of sand only. All the other members of this family which I have examined, including the large *Strombus gigas* at Bermuda, have similar habits and live on a sandy bottom. On the other hand, the large carnivorous genera, *Cassis* (helmet shell) and *Melo* (bailer), which also live on a sandy bottom, are always found almost buried in it, and plough their way through the sand by means of a large creeping sole. *Trochus niloticus*, which feeds on the encrusting algae of coral boulders (see Moorhouse, Vol. III, No. 5), crawls over these by means of its creeping sole.

(*b*) Feeding Mechanism and Food.

Pterocera is a " scraping " Gastropod (Yonge, 1928*a*), the buccal armature consisting of " a pair of laterally-placed gelatino-chitinous jaws " (Woodward, 1894) and an odonto-phore. The radula is very small and delicate for so large an animal; it is not more than $1\frac{1}{2}$ mm. broad in a full grown-animal. Cooke (1895), who states (p. 218) that the four recent genera of the Strombidae. *Strombus, Pterocera, Rostellaria* and *Terebellum*. all have a radula of the same general type, describes this (p. 418) as " central tooth with strong median cusp, marginals falciform, slender, edge more or less denticulate." It is obviously the radula of an herbivorous animal, and of one which does not scrape the extensive, hard surfaces worked over, for example, by the broad, many-toothed radula of *Trochus niloticus*.

The feeding of *Pterocera* was studied by placing the animals in large glass dishes together with a selection of algae and of the eel grass. *Cymodocea*. The animals lurched about in an ungainly manner, with the proboscis and the long optical stalks with the terminal eyes projecting in a somewhat ludicrous manner from under the anterior end of the shell. They fed readily when weed was placed between them and the end of the dish, against which the spines of the shell rested. Under these conditions the proboscis is extroverted slightly, exposing the small, weakly armoured radula. This is then employed to " nibble " off the very finest algae, usually the red weed which grows epiphytically on the large brown algae, in the same manner that *Polysiphonia* grows on *Fucus* in this country. The radula was quite incapable of eating even moderate-sized algae, such as the common brown algae, *Sargassum* or *Turbinaria*. *Pterocera* is clearly exclusively herbivorous, browsing upon the most delicate fronds of algae and on the other animals and plants which occur on this. It is quite defenceless and very slow-moving, and relies for protection on its very thick shell and strong operculum.

Examinations of the stomach contents confirm the observations on feeding. The dark brown fluid contained large quantities of minute pieces of delicate algae, with some fine sand and a few very small crustacea and occasionally a nematode. Crustacea and nema-todes were in several instances found still alive. Both the sand and the animals would certainly be obtained from the weed. Woodward, who examined the stomach contents of a preserved *Pterocera* (collected by Haddon in the Torres Strait), found that plant remains were abundant, " especially threads of blue-green algae and brown sea-weeds ; in addition there were a quantity of sand-grains, sponge spicules, a few small Crustacea, and numerous large Foraminifera of the genus *Orbiculina*." He thought that the last-named might be of use in trituration, as well as supplying part of the calcium for the shell. As will be shown later, there is no reason why *Pterocera* should possess a triturating mechanism in its stomach, nor is this fitted for such a function.
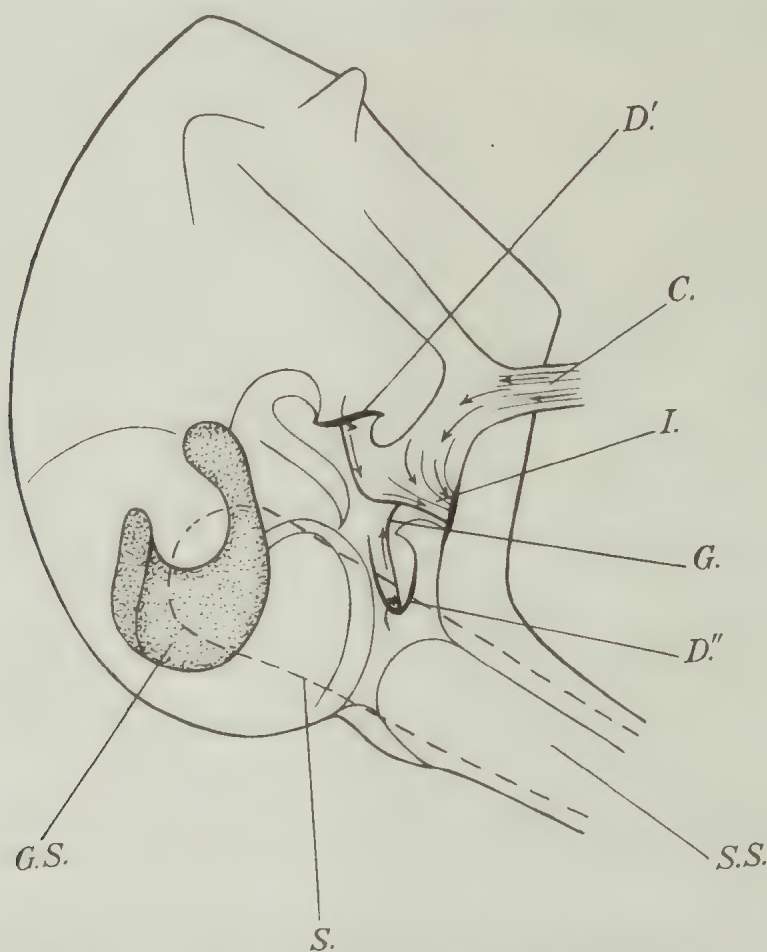
(*c*) Stomach and Crystalline Style.

The anatomy of the digestive system of *Pterocera* has been described by Huxley (1853), and later, in more accurate detail, by Woodward (1894). The original observations in this paper are concerned with the ciliary currents in the living stomach, and the relation of this to the style-sac and digestive gland.

The small buccal mass is succeeded by a short, narrow oesophagus, on the sides of which lie a pair of small salivary glands, which open into the buccal cavity. All of these

lie within the proboscis. Continuing in the words of Woodward: " The oesophagus, on entering the body, becomes suddenly enlarged to form the crop; this structure, which is about 4½ in. long, tapers gradually away into a small tube, and is situated, together with the anterior aorta, in a narrow channel-like body-cavity hollowed out of the great anterior muscular mass of the body; from this it passes into the coiled visceral mass, and running through the liver becomes slightly funnel-shaped and enters the stomach."

The anatomy of the stomach, after being opened up along the mid-dorsal line, is shown in Text-fig. 1. The crop (c.) enters about the middle of the stomach and on the dorsal

TEXT-FIG. 1.—*Pterocera crocata;* stomach opened along the mid-dorsal line. × 4. c., crop; D'., D''., ducts of digestive gland; G., grooves leading out of the ducts from the digestive gland; G.S., gastric shield; I., entrance to intestine; S., crystalline style (indicated by broken line); S.S., style-sac. Arrows indicate direction of ciliary currents.

side. The walls are ridged and ciliated, the cilia carrying material (probably with the aid of peristalsis) into the stomach as indicated by the arrows. The intestine (I.) leaves the stomach a little anterior to this. It is a very narrow tube which, after curving round the anterior border of the digestive gland and passing under the kidney, merges into the much wider rectum, which opens by a narrow anus into the mantle cavity. On the floor of the stomach and near to the openings of the crop and intestine are the two ducts of the digestive gland (D'., D''). The very large style-sac (S.S.) opens at the anterior end of the stomach. It contains a large, exceptionally firm style, and is *entirely separate* throughout from the intestine.

The Strombidae contain the largest styles of all the Gastropoda. In *Pterocera crocata*

(not the largest species of this genus), a fully grown animal whose shell, including the spines, was 18 cm. long, the style was 8 cm. long and 3 mm. in diameter at the head end. *Strombus gigas*, the largest of the Strombidae, and probably the largest *herbivorous* gastropod, contains an even larger style. A specimen examined at Bermuda (Yonge, 1932) which had a shell (which has no spines) 11½ in. long, possessed a style 22·25 cm. long, 6 mm. wide, and weighing 2·78 grammes. It has been known for a long time that the styles in some species of Lamellibranchs and Gastropods disappear from time to time, and then are re-formed (which is responsible for the old view, held by Woodward amongst others, that the style is a reserve of food), whereas in other species they are always present. This difference has been shown to be correlated with the absence or presence respectively of a separate style-sac (Yonge, 1925, 1926*a*, 1926*c*). When animals possessing a style which is formed in a sac which communicates throughout its length with the intestine are exposed to conditions which cause a lowering of the metabolism, the style is no longer secreted at the same speed as it is dissolved by the less acid contents of the stomach. In consequence it is soon completely dissolved, for, being composed of a protein which is only solid at a lower pH than that present in the stomach and intestine, it is only maintained in these animals as a result of a delicate balance between the rate of its secretion by the cells lining the style-sac and the rate of its dissolution in the stomach. In animals where the style-sac is separate from the intestine, only the head end of the style is dissolved when secretion is stopped by a lowering of metabolism. In previous work on the gastropod *Crepidula* (Yonge, 1925), where the style lies in a groove alongside the intestine, it was shown that the style disappears entirely, for reasons given above, when the animals are removed from water for one or two days, but is re-formed exactly as in lamellibranchs such as *Mytilus* and *Ostrea* when it is returned to water. When the style was absent the pH in the stomach rose from 6·0 to 7·025, for it is the dissolution of the style substance which is responsible for the low pH of the stomach contents—a pH which is about the optimum for the working of the amylase which is released when it dissolves. The style of *Crepidula* has a pH of 5·8, and dissolves with increasing speed as the pH of the water rises higher than 4·0 ; below that point it is not dissolved.

The style of *Pterocera* has a pH of about 5·4. Two animals were taken out of water and kept in the comparatively cool aquarium for four days. At the end of this period one was dead and the other showed slight traces of life. But in both the style was *intact* and firm throughout, even the head end, which lies in the stomach, being only slightly dissolved. Exactly the same results were obtained previously in experiments on the Lamellibranchs, *Mya* and *Ensis* (Yonge, 1925), which both have separate style-sacs. In Gastropoda, therefore, as well as in Lamellibranchia, the permanence of the style is correlated with the presence of a separate style-sac.

The style-sac in *Pterocera* extends, as Woodward has shown, through the digestive gland, " over the anterior aorta, and, passing close to the left of the pericardium, enters the dorsal mantle wall, down which it extends just to the left of the osphradium, nearly the whole length of the gill, where it ends abruptly." The head of the style (s.) as indicated by the broken lines in Text-fig. 1, projects out of the style-sac into the lumen of the stomach, where it bears against the prominent gastric shield (G.S.). This structure is invariably present in all molluscs which possess styles, and is always especially large and strong in those which have the particularly firm styles formed in separate style-sacs.

Apart from the region around the openings of the crop, the intestine and the ducts

of the digestive gland, there is little sign of ciliation in the stomach. The region immediately posterior to the gastric shield is unciliated, as in all molluscs with styles. The large, distal region of the stomach, called the cardiac region by Woodward, is either unciliated, or possesses short, very weakly beating cilia. The manner in which the stomach works can easily be seen by reference to Text-fig. 1. Material enters from the crop, and is then whirled round in the lumen by the rotating action of the style. Digestion then takes place, enzymes being liberated from the salivary glands, the crystalline style and, possibly (for reasons given in the next section), from the digestive gland. This latter organ is primarily, however, an organ of absorption and intracellular digestion, as are the digestive diverticula in the Lamellibranchs (Yonge, 1926*b*). Ciliary currents carry dissolved matter and very fine particles into the ducts of the digestive gland, while at the same time powerful currents carry waste matter (material not assimilated by the cells of the digestive gland and the indigestible remnants after intracellular digestion which are rejected by the cells) out of the ducts by way of grooves (G.) on the floor of the ducts. These grooves are the continuation of similar grooves from each of the many tubules of the digestive gland. The ingoing currents enter above, and in this way a continuous current is maintained in exactly the same manner as in the ducts and diverticula of the lamellibranchs (Yonge, 1926*b*, 1926*c*). The grooves from the two ducts unite with one another, as shown in Text-fig. 1, and then pass into the intestine. All relatively large particles, such as sand grains, which are found in large numbers in the rectum, which have resisted the action of the digestive enzymes in the stomach, are also carried by ciliary currents into the intestine and thence to the rectum, from which they are ejected at the anus.

The mechanism of the stomach of *Pterocera* is essentially similar to that of the lamellibranchs which have been examined, *e. g. Modiolus* (Nelson, 1918), *Mya* (Yonge, 1923), *Ostrea* (Yonge, 1926*c*) and *Ensis* (Graham, 1931). The stomach is an organ for digestion and for the sorting out of fine from large particles, the former passing into the ducts of the digestive gland and the latter into the intestine. No trituration is possible in a stomach which is embedded in the tissues and has little surrounding muscle, nor, as will be shown more clearly in the next section, is such action necessary, the plant food, which clearly forms the staple diet of the animal, being broken down by enzymatic action. The main difference between this stomach and those of the lamellibranchs mentioned above lies in the absence of the food-sorting caecum which is so characterstic of those animals.

(*d*) DIGESTIVE ENZYMES.

A series of qualitative experiments were carried out to determine the nature of the digestive enzymes in the stomach, and further experiments on extracts of the crystalline style, digestive gland and salivary glands, to determine the origin of the enzymes found in the stomach. Table I gives the results of a series of experiments on the stomach contents, the pH of which was about 5·9.

The enzymes in the stomach of *Pterocera* are apparently confined to those which act on carbohydrates and fats, since a protease was not found. Fats are only digested very slowly, but starch and glycogen are digested at great speed, sucrose rather more slowly, and, most important of all, *a powerful cellulase is present*.

Further experiments were carried out to confirm the presence of this cellulase, and in every case with success, the filter-paper used as a substrate being invariably broken down to a mush of separated fibres and a strong reduction with Fehling's solution denoting the

TABLE I.

Fluid taken from the stomachs of 20 *Pterocera*, filtered twice, and the clear brown fluid
obtained made up to 100 c.c., half of which was boiled and used for control experiments.

Extract.	Substrate.	Time.	Result.
5 c.c.	5 c.c. sea-water	4 days	No reduction with Fehling's solution.
	Control .	,,	No reduction.
5 ,,	5 c.c. 1% starch	1 day	Strong reduction.
	Control .	,,	No reduction.
5 ,,	5 c.c. sat. soln. glycogen .	,,	Strong reduction.
	Control .	,,	No reduction.
5 ,,	5 c.c. 5% sucrose .	,,	Good reduction.
	Control .	,,	No reduction.
10 ,,	0·125 grm. filter-paper .	4 days	Strong reduction ; paper reduced to mush.
	Control .	,,	No reduction ; paper intact.
10 ,,	0·2 grm. fibrin .	23 days	Fibrin intact.
	Control .	,,	,, ,,
10 ,,	5 c.c. olive oil emulsion .	,,	Slight production of fatty acids.
	Control .	,,	No production of fatty acids.

formation of sugar. The osazone test was applied at the end of four days' incubation
(carried out in all cases in the aquarium) and yielded abundant crystals of glucosazone.
After the addition of an equal part of 40% NaOH no reduction was given with Fehling's
solution. This shows the absence of maltose, and apparently the cellulose is broken down
to glucose without the intermediate formation of maltose. Other experiments were
conducted using pieces of the brown alga. *Hydroclathris*, and of the eel grass, *Cymodocea*,
as substrate. No action was found on *Cymodocea*, the pieces remaining intact after 12 days,
but *Hydroclathris* was quickly reduced to small, soft pieces, the process being obvious to
the naked eye after 4 days, and almost complete after 12 days. In the control experiments
both *Hydroclathris* and *Cymodocea* remained intact after 12 days.

Finally an experiment was carried out to determine the optimum pH for the working
of the cellulase. Details of this experiment are given in Table II. I am indebted to
Mrs. Yonge for the actual sugar estimations.

TABLE II.

11 c.c. of fluid removed from the stomachs of 43 *Pterocera*, filtered and made up
to 200 c.c. with filtered sea-water. 20 c.c. of this fluid used for each experiment with
0·25 grm. of torn-up filter-paper and acid or alkali and water to make up 25 c.c. in all ;
3 c.c. removed for pH determinations in all cases. Toluol added to each experiment.

No.	HCl.	NaOH.	Water.	Initial pH.	Percentage of glucose after 3 days as determined by McLean's method.
I.	1·5 c.c. ·1 N.	..	3·5 c.c.	3·1	0
II.	1·0 ,, ,,	..	4·0 ,,	3·8	·046
III.	0·75	..	4·25 ,,	5·1	·078
IV.	0·50 .. ,,	..	4·5 ,,	5·35	·078
V.	0·25 ,, ..	..	4·75 ,,	5·85	·098
VI.	..	..	5·0 ,,	6·7	·065
VII.	..	0·05 c.c. ·1 N.	4·95 ,,	7·35	·059
VIII.	..	0·1 .. ,,	4·9 ,,	7·8	·033
IX.	..	0·25 ,, ,,	4·75 ,,	8·35	0
X.	..	0·5 ,, ,,	4·5 ,,	9·05	0

The results of this experiment are shown graphically in Text-fig. 2. and reveal that there is a well-marked optimum for the action of the cellulase at pH 5·85. which is about the pH of the fluid in the stomach.   It also agrees fairly closely with the optimum pH of 5·28 for the working of the cellulase from *Helix* found by Karrer and Illing (1925).   The presence of this cellulase. found only in very highly specialized herbivories. *e. g. Helix* and also the wood-boring Teredinidae (Harrington. 1921 ; Potts. 1923 ; Dore and Miller. 1923 ; Yonge. 1926*b* ; and Boynton and Miller. 1927). appears to be widespread in the Strombidae, for experiments on *Strombus gigas* at Bermuda revealed the presence of a powerful cellulase.   By the aid of this enzyme (the presence of which renders mechanical trituration unnecessary). the pieces of algae rasped off by the radula are broken down in the stomach, the glucose so formed being absorbed and the contents of the cells released for further
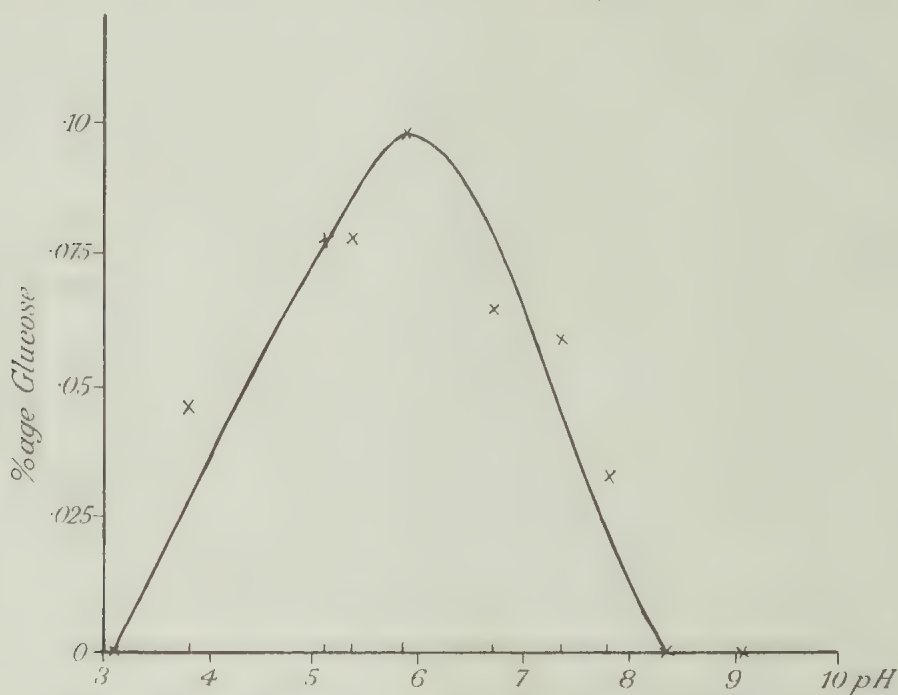
TEXT-FIG. 2.—Graph showing digestion of cellulose (filter-paper) at various pH by cellulase from the stomach fluid of *Pterocera crocata*.   See Table II.

digestion in the stomach if they are carbohydrates or fats or, if protein, for conduction to the tubules of the digestive gland. where they are ingested and digested intracellularly. *Pterocera crocata*. and the Strombidae in general. are thus amongst the most highly specialized of the herbivorous Gastropoda.

Experiments with extracts of styles revealed an amylase which digested starch and, rather less readily. glycogen. but not sucrose or cellulose.   This is in agreement with the work of various authors on the styles of Lamellibranchs (see Yonge. 1931. 1932*b* for details). Extracts of the digestive gland digested starch. glycogen and sucrose readily, a very strong reduction of Fehling's solution being given after 2 days' incubation.   There was no indication of the digestion of cellulose after 20 days' incubation.   A lipase was identified, but. even after 20 days. no digestion of fibrin took place.   This apparent absence of a protease agrees with the results of work by Krijgsman (1928) on *Helix*.   He found no protease in the gut and only very slight traces of protease in extracts of the digestive

gland, and he suggests that only soluble proteins are taken in by the absorbing cells of the gland, and that digestion is completed within these cells by proteases which are difficult to extract. A somewhat similar state of affairs would appear to exist in *Pterocera*, where, as in *Helix*, the cellulase will liberate the soluble proteins from the cell-sap of the plant food. But in *Pterocera* intracellular digestion of small particles probably occurs, whereas Krijgsman was unable to find this in *Helix*.

The salivary glands in *Pterocera* are very small and difficult to excise. Accordingly extracts were made of the entire buccal mass. These revealed an enzyme which digested starch and glycogen, but not sucrose or cellulose. This again agrees with the work of Krijgsman on *Helix*, the salivary glands of which also secrete a powerful amylase. The origin of the cellulase is as difficult to determine in *Pterocera* as it has been in *Helix*. It is possible that in both cases it is produced by the salivary glands, but either some other method of extraction is needed to obtain it (all these extractions were in filtered sea-water), or else, like the protrypsin of Vertebrata, it needs some activating agent. Of the presence of this powerful enzyme in the gut contents of both *Pterocera crocata* (also *Strombus gigas*) and *Helix* there is no doubt whatever.

From the results of the experiments recorded above the process of digestion in *Pterocera*, and probably in all the Strombidae, may be reconstructed. The plant food obtained by the rasping of the delicate radula passes first into the crop, where it is acted on by the sucroclastic enzymes from the salivary glands, which may include the cellulase. These enzymes are also carried into the stomach with the food, and there they are reinforced by the amylase from the style and by a sucrase, and probably a weak lipase, from the digestive gland. The cellulase breaks down the cellulose walls of the plant tissues, and exposes the starch and fats within to the action of the amylase and lipase. Proteins cannot be digested in the stomach owing to the absence of a protease. This enzyme, as already emphasized elsewhere (Yonge, 1930), is *never* present in the stomachs of molluscs possessing styles, and *cannot* be present because the style composed of a globulin which is readily attacked by a protease could not exist in the presence of such an enzyme. Such animals can *never possess any extracellular proteoclastic enzymes*, and so, to the extent that they are unable to break down the bodies of animal prey by enzymatic activity, are invariably *specialized herbivores*. The Septibranchia, which possess a crushing gizzard, and only a small style which is probably vestigial, are able to break down animal prey mechanically but not chemically (Yonge, 1928*b*).

Absorption of the products of the digestion of carbohydrates and fats, namely glucose and fatty acids with glycerol respectively, takes place probably exclusively in the tubules of the digestive gland. Sections of this reveal the presence of many oval-shaped concretions which often almost fill the cells. These may be enzymes about to be secreted, but are more probably the indigestible remnants of intracellular digestion, which are finally ejected and passed into the stomach and so into the intestine and out of the body. There are smaller rounded bodies which stain red with safranin and may be secretion or ingested food. It is certain that protein, either in solution or, more probably, as minute fragments, must be ingested and digested intracellularly in the cells of the digestive gland. The three processes of feeding, digestion and assimilation all reveal the high degree of specialization attained by *Pterocera*, and probably all the Strombidae, as herbivores.
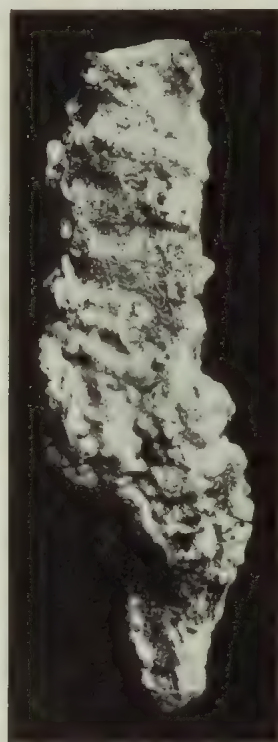
3. VERMETUS NOVAE HOLLANDIAE.

(a) Occurrence and Habits.

This animal, for the naming of which I am indebted to Mr. G. C. Robson, appears to be the largest of the Vermetidae, and was found only on the outermost barrier reefs. The specimens on which this work was done were collected on Ruby Reef, and others were taken by the Shore Party on Yonge Reef. It is one of the few Gastropoda which live on the surface of these low outer reefs which are fully exposed to the Pacific surf, and in both localities was found only on the inner side of the reef crest (Ruby Reef), and in the anchorage coral zone (Yonge Reef), which is illustrated in Plate XXIV, fig. 1 of Paper 2 in Vol. III of these reports. It was never found on any of the inner barrier reefs or on the reefs

TEXT-FIG. 3.

TEXT-FIG. 4.

TEXT-FIG. 3.—*Vermetus novae hollandiae*: animal removed from the shell, showing operculum, buccal mass and mantle edge. × ⅔.

TEXT-FIG. 4.—*Vermetus novae hollandiae*: shell taken from Ruby Reef showing encrustation of *Lithothamnion* and the absence of the terminal whorls characteristic of *Magilus*. The actual length of this shell was 24 cm. ×. ⅓.

surrounding low wooded islands in the Lagoon Channel, where, in view of its exceptional size, it would hardly have escaped notice had it been present. It grows firmly cemented to dead coral rock. The tube, as shown in Text-fig. 4, is never coiled, and frequently almost straight, and is usually covered over with encrusting Lithothamnia, Madreporaria or *Polytrema*, only the wide, circular opening with the dark brown operculum revealing its presence. The largest specimen collected had a shell 28 cm. long, the internal diameter of the opening being 3·6 cm. The terminal 7 cm. of the shell were not occupied by the animal, but cut off by a series of five partitions. The length of the contracted animal (Text-fig. 3) after removal from the shell was 11 cm. and the diameter of the operculum 2·5 cm.

(b) Feeding Mechanism.

The exact mode of feeding in the Vermetidae has long been a matter of speculation. Lacaze-Duthiers (1860) and Houssay (1884) both drew attention to the great size of the pedal gland in these sessile animals, but Rougemont (1880) was the first to suggest that food might be collected in the mucus strings secreted by this organ. Simroth (1901) accepted this view, but later authors threw doubt upon it. Finally Boettger (1930), working on *Vermetus* (*Serpulorbis*) *gigas* obtained from Rovigno and Naples, has reinvestigated the subject, and his results entirely confirm those of Rougemont and Simroth. His paper was published after the work described in this paper was completed, and, as will appear, it is possible that he described a part, and not the whole, of the feeding mechanism. My own investigations will first be described, and then Boettger's results discussed in the light of these.

The behaviour of animals placed in large glass dishes with clean sea-water was first studied. When the animals were fully expanded the operculum projected slightly beyond the opening of the shell, the opening of the pedal gland (o., Text-figs. 5 and 6), the pedal tentacles (T.), the mouth (M.), anterior end of the buccal mass (B.) and of the mantle (Ma.) all being exposed. While it is being extruded the buccal mass is on the right-hand side of the shell looking at it from above, but when fully expanded it twists round until it is dorsal, and then usually proceeds to revolve slowly one way and then the other through an arc of about 90°. A current of water, created by the lateral cilia on the gills (G.), is drawn in continuously on the left-hand side of the mantle cavity, as indicated by the large arrow in Text-fig. 5, while an exhalent current is ejected on the right-hand side. The presence of these powerful currents is readily detected with carmine.

A continuous stream of mucus is poured out from the opening of the pedal gland, and forms masses (Mu.) which hang down outside the operculum. Food, such as plankton or fine pieces of weed, sticks tightly to this, but in spite of repeated experiments the animals were *never* seen to swallow or even to attempt to swallow this. There was apparently no means of drawing these mucus strings back to the mouth, and the introvert was incapable of stretching even as far as the edge of the operculum. Whenever the animals drew back within their shells, which they did frequently, the mucus strings were cut off between the edge of the operculum and the side of the tube. In the course of time the bottom of the dish was littered with mucus to which particles adhered, but no food was ever obtained in this manner, nor was any freely swimming plankton ever seen to be so captured.

The obvious inability of *Vermetus* to capture food in this way led to an examination of the interior of the mantle cavity. Animals were removed from their shells (see Text-fig. 3) and the mantle cavity exposed, as shown in Text-fig. 5, by cutting it away on the right-hand side. An examination, by means of suspensions of fine carborundum powder and of carmine, of the ciliary currents revealed that essentially the same mechanism for food collection is present as that described by Orton (1912) in *Crepidula*, *Calyptraea* and *Capulus*.

The mantle cavity is divided into two horizontally by the gills (G.). The lateral cilia on the sides of the gill filaments beat upwards, causing a current to pass through the gills in that direction. As a result water is drawn into the inhalent chamber between the gills and the ventral surface of the body, strained through the gills, and then expelled by way of the exhalent chamber between the upper surface of the gills and the mantle. The whole

process, as Orton has pointed out for *Crepidula*, is essentially the same as in the Lamellibranchia. The gills consist of a single row of filaments, each of which is laterally compressed and tapers towards the tip, the whole series forming a compact row. As in *Crepidula*, there is an endostyle (E.) at the base of the gills. This secretes a copious supply of mucus, which is carried on to the surface of the gills by ciliary
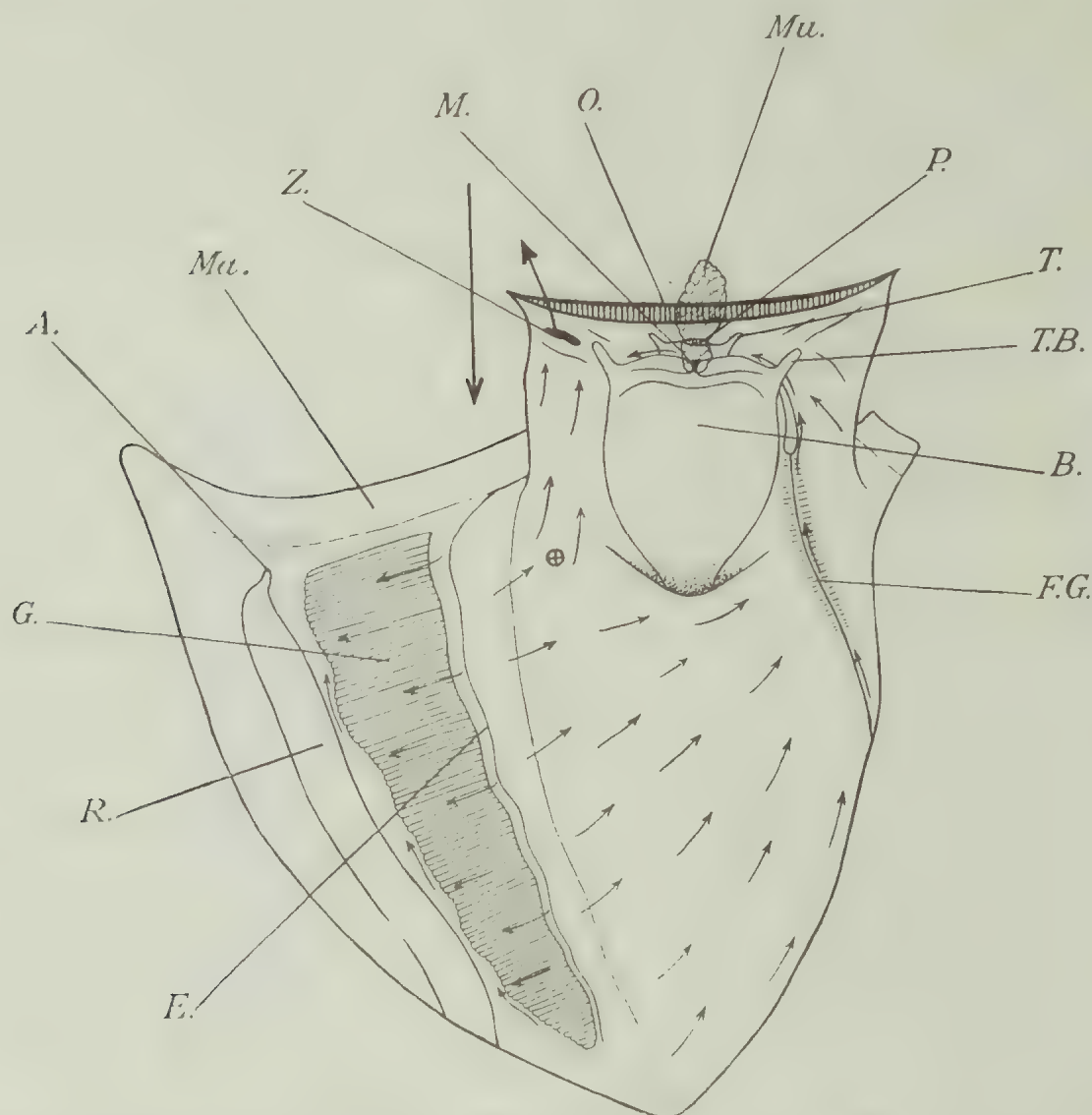
Text-fig. 5. *Vermetus novae hollandiae*; mantle cavity exposed by cutting of the mantle along the right-hand side. × 2¼. A., anus; B., buccal mass; E., endostyle; F.G., food groove; G., gills; M., mouth; Ma., mantle; Mu., mucus from pedal gland; O., operculum; P., aperture of pedal gland; R., rectum; T., pedal tentacle; T.B., tentacle on buccal mass; ⊕, beginning of rejection currents for heavy material; Z., site of accumulation of waste matter. Small arrows indicate direction of ciliary currents, large vertical arrow position of inhalent current.

action. The cilia on both the frontal (ventral) and abfrontal surfaces of the gills beat towards the tips, so that particles in suspension which are intercepted by the gills are carried to their free margins. Here there is a current which carries them forwards. In life the free margin of the gills lies in close connection with a food groove (F.G.) on the right-hand side of the floor of the mantle cavity. Material is transferred to this from the gills and is carried towards the mouth. Heavier material which is drawn into the inhalent chamber and there settles to the bottom is caught in currents on the floor of the chamber (indicated

by the arrows in Text-fig. 5), and also transferred to the food groove. Still heavier material which falls almost immediately after being drawn in is carried outwards from the point ⊕ on the left-hand side of the buccal mass (B.), and collects in masses (z.) immediately behind the operculum. These masses are from time to time ejected, as indicated by the large arrow, as a result of convulsive movements of the mantle. This rejection of waste material from the inhalent chamber is also a universal feature in the Lamellibranchia.

Material which enters the food groove, either from the floor of the inhalent chamber or from the gills, is carried round the right-hand side of the buccal mass to the mouth (M.). As the food streams approach the mouth the small introvert is extruded over the opening of the pedal gland (P.). At the same time the mouth opens and the radula is exposed; this seizes the food which has become mixed with mucus from the pedal gland and draws this into the mouth, which then closes. If there is an excess of food this is passed beyond the mouth, and joins the other material which is rejected from the left-hand side of the mantle cavity. All this was observed repeatedly after the animals had been exposed as shown in Text-fig. 5. When fed with material in suspension while still in the shell they invariably drew back into the shell about half a minute after the food had entered the mantle cavity.

There can be no doubt that *Vermetus novae hollandiae* feeds *only* in the manner described, the mucus from the pedal gland being used exclusively to increase the bulk of the finely divided food so that the radula can grasp it. This is clearly necessary, for the radula is primarily an organ for rasping or boring, and not naturally adapted for the collection of fine particles and mucus strings except in a few cases, such as *Aporrhais pes-pelecani* (personal observation), where it is associated with a sucking proboscis.

Boettger found that the stomach contents of *V. gigas* consisted of fine plankton embedded in mucus. He states definitely that there are no ciliary currents such as occur in the Lamellibranchia or in the tube-dwelling worms. He does not state that he examined the mantle cavity. The results of his experiments appear to show definitely that in this species food *is* caught in the mucus strings, which can extend for up to 30 cm., and may be three or four in number. Plankton animals are caught in these threads, which are then drawn back towards the mouth and seized by the powerful radula. He found a definite relation between the time the threads had been out and their withdrawal. He failed to find any poison in the mucus, the secretion of which was only promoted by the presence of living plankton, and not by dead plankton or meat-juice. He regarded the pedal tenacles as the receptors of this stimulus. In addition to this mode of feeding, Boettger states that *Vermetus* can feed on large prey which comes by chance within the range of its mouth.

Clearly conditions are very different in the two species. Boettger explicitly states, however, that in *V. gigas* food collection can only occur in *still*, or almost still, water. Where *V. novae hollandiae* lives the water is *never still*, which was forcibly demonstrated by the strength of the Pacific surf on Ruby Reef when I visited it, and even when placed in bowls of still water it *never* feeds by means of its mucus strings. Exactly the same results were obtained with a smaller species of *Vermetus* common on Batt Reef and other inner barrier formations. These animals also were invariably found on the surface of the reefs, fully exposed to the turbulent water which washes over, particularly when the tide is rising or falling. There can be no doubt that these two species of *Vermetus* are *exclusively ciliary feeders*, collecting phytoplankton and fine particles generally from the water. *Vermetus gigas* clearly has a different feeding mechanism. In the light of my results the ciliation

in the mantle cavity of *V. gigas* should be examined. Judging by figures given by Lacaze-Duthiers. the gills are small. If it is found to be similar to that in *V. novae hollandiae*, then it will be proved to have two means of collecting food—by mucus strings and by ciliary currents. the former being an adaptation to life in very still waters. If there is no ciliary mechanism in the mantle cavity. the differences between the two species would be so great as to demand a revision of the taxonomy of the Vermetidae.

(c) ALIMENTARY CANAL.

In Text-fig. 6 is shown a *Vermetus* dissected to display the alimentary system, the direction of the ciliary currents being indicated by arrows. The mouth gives access by way of the buccal mass which contains the radula (Ra.) and jaws. and into which open a pair of salivary glands. to a long. thick-walled oesophagus (Oe.). The cilia in this region, which beat posteriorly. are comparatively. weak and the passage of food through this region is probably assisted by peristalsis. Posteriorly the oesophagus merges imperceptibly into a thin-walled region with powerful cilia which may be designated a crop (C.). Except for the region around the gastric shield (G.s.) the stomach (St.) is everywhere ciliated. Material entering from the crop is carried towards the gastric shield against which in life the head of the style rests. and to the three openings of the digestive gland (D'.. D''.. D'''.). Ciliary currents lead away from these but. as frequently happens. ingoing currents are difficult to determine. Excess or waste material is carried into the intestine (I'.). the opening of which is close to that of the crop and separated by a ridge from the cavity of the stomach. In the intestine are powerful ciliary currents. The style-sac (S.s.) is in restricted connection throughout with the intestine. and extends for about one-third of the length of the latter. the two cavities being separated by prominent typhlosoles. Cilia within it cause the style to rotate in an anti-clockwise direction when viewed from the stomach. After the termination of the style-sac. the intestine describes a loop (I''.) before again turning anteriorly and merging into the wide rectum (R.). This possesses a ventral groove in which is a strong ciliary current which conducts the faeces to the anus (A.). The faeces consist of small elongated pellets. each enclosed in a mucous envelope with twisted ends. They contain fine particles—the largest being minute sand-grains - fine. colourless strands of algae. and great masses of very small rounded bodies. brown or yellow in colour. which are extruded. the indigestible remnants of intracellular digestion probably. from the digestive gland. No evidence of animal remains was ever found in the faeces.

Unlike *Pterocera*. the style. which is in free communication with the intestine. and so liable to be dissolved by the fluid in this should the rate of secretion be lowered. dissolves entirely after the animals have been out of water for a short time. Indeed it was impossible to find a style in animals which had been kept in the aquarium for more than a few days.

The structure of the alimentary canal is clearly correlated with the food and feeding of this species. The presence of a style indicates that the animal has no free protease in the stomach. and that it is a specialized herbivore feeding on finely divided food. No time was available for experiments on digestive enzymes. but everything indicates that conditions are essentially the same as in *Pterocera*. carbohydrate and possibly fat being digested in the cavity of the gut. and fine particles of protein being carried into the tubules of the digestive gland and there ingested and digested intracellularly. Animal food, such
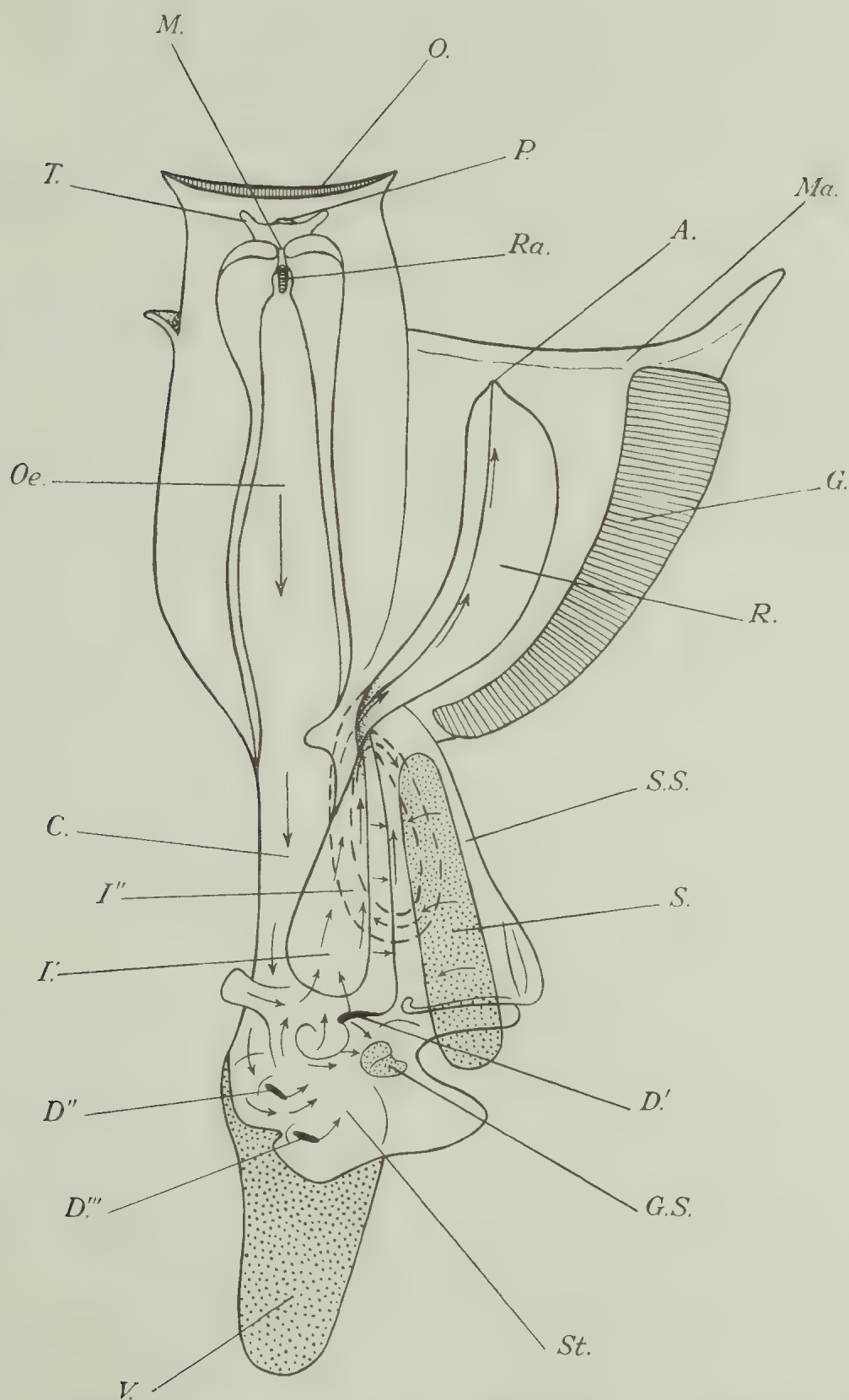
TEXT-FIG. 6.—*Vermetus novae hollandiae*; alimentary canal exposed. ×1½. C., crop; D'., D''., D'''., ducts of digestive gland ; G.S., gastric shield ; I'., I.'', intestine ; Oe., œsophagus ; Ra., radula ; S., crystalline style ; S.S., style-sac ; St., stomach ; V., visceral mass containing gonad.   For other lettering see previous figure.

as Boettger states is taken by *V. gigas*, could not be utilized by *V. novae hollandiae*, because this animal could neither break this up chemically, by proteases, nor by mechanical means. Examination of the stomach contents revealed only mucus and excrement from the digestive gland. Lacaze-Duthiers (1860), who gives a general account of the alimentary system in *V. gigas*, makes no mention of anything corresponding to a style or style-sac. He may have overlooked this, but in any case the anatomy of the alimentary system in this species needs closer study, since, from Boettger's findings, it must clearly have other means for digesting food than are present in *V. novae hollandiae*. The taxonomy of the Vermetidae appears to require further investigation.*

Some confusion exists between the large species of *Vermetus* which live on the surface of reefs and *Magilus*, which grows up actually embedded in living coral, the last whorl of the shell increasing in length with the growth of the coral. So far as can be found, the anatomy of *Magilus* has never been adequately described and little is known of its habits. It is an Indo-Pacific genus, but was never found by us on the Great Barrier Reef. By the courtesy of the British Museum (Nat. Hist.) I have been able to examine a preserved specimen (*Magilus*, sp.) kindly forwarded to me by Mr. G. C. Robson. The shell with its terminal spiral and absence of encrusting growths is totally unlike that of *Vermetus*. The resemblance lies in the operculum, which in both genera is usually the only indication of their presence in nature, but even here the operculum of *Magilus* is oval and not round. It proved impossible to determine the mode of feeding. Radula and jaws are absent, but there is no certain indication of a ciliary feeding mechanism. Examination of the living animal might reveal this. No sign of a style-sac or a gastric shield was found in the alimentary canal (not very well preserved), and this indicates that the animal is probably not a ciliary feeder. As shown later, all the Gastropoda known to feed by ciliary currents possess styles. It is possible that the animal may possess a sucking pharynx and feed on the tissues of the coral, or take zooplankton seized by the tentacles of the polyps. A study of the feeding and other habits of *Magilus* and of the other members of the family Coralliophilidae would be of the greatest interest.

4. OCCURRENCE OF THE CRYSTALLINE STYLE IN GASTROPODA.

Various authors, notably Robson (1922*b*) and Mackintosh (1925), have reviewed the literature on the presence of the crystalline style in members of the Gastropoda. Both of these authors were principally concerned with the morphological or the taxonomic aspects, and did not consider in any detail the correlations between the presence of the style and the feeding habits and food of the animals. Mackintosh thought that since the food of *Crepidula* is identical with that of the oyster, " the retention or appearance of a style in certain gastropods might be correlated with the feeding habits." Experiments which he carried out met with no definite results. In view of more recently published work on this subject, here and elsewhere (see Yonge, 1931, 1932*b* for details), and of the greater knowledge we now possess on the function of the crystalline style in Lamelli-branchia, a further review of the subject from the physiological aspect is now necessary.

In Table III are listed the genera of Gastropoda in which crystalline styles are known to occur. So far as this is available data are given on the habitat of the animals, mode of feeding, food, and on the character of the style-sac.

* See note on p. 281.

TABLE III.—*Presence of a Crystalline Style in the Gastropoda.*

Sub-order.	Family.	Genus.	Habitat.	Feeding mechanism.	Food.	Style-sac.
Docoglossa						
Rhipidoglossa	Fissurellidae	*Fissurella* (Haller, 1888)	Marine	Radula	Encrusting algae	C
,,	Neritidae	*Neritina* (Lenssen, 1899)	Freshwater	,,	?	C
Taenioglossa	Ampullariidae	*Ampullaria* (Bouvier, 1880)	Amphibious	,,	Algae	?
,,	Pomatiidae	*Pomatias* (Garnault, 1887)	Terrestrial	,,	Vegetation	C
,,	Rissoidae	*Rissoa* (Simroth, 1901)	Marine	,,	Algae[1]	?
,,	Adeorbiidae	*Adeorbis* (Woodward, 1899)	,,	,,	,,	S
,,	Assimineidae	*Assiminea* (Seshaiya, 1932)	Brackish water	,,	?	RC
,,	Hydrobiidae	*Hydrobia* (Robson, 1922a)	Ditto	,,	Weed	RC
,,	,,	*Hypsobia* (Robson, 1921)	Freshwater amphibious	,,	,,	RC
,,	,,	*Bithynella* (Bregenzer, 1916)	Freshwater	,,	?	?
,,	,,	*Lithoglyphus* (Von Ihring, 1885)	,,	,,	?	S
,,	,,	*Bithynia* (Moquin Tandon, 1855; Seshaiya, 1932)	,,	,,	?	RC
,,	,,	*Mysorella*	,,	,,	Diatoms	RC
,,	,,	*Amnicola* (Seshaiya, 1929b, 1930)	,,	,,	?	RC
,,	Melaniidae	*Spekia*	,,	,,	? Weed	S
,,	,,	*Tanganyicia*	,,	,,	,,	S
,,	,,	*Limnotrochus*	,,	,,	,,	S
,,	,,	*Chytra* (Moore, 1898a, 1899a; Digby, 1902)	,,	,,	,,	S
,,	,,	*Melania* (Mackintosh, 1925)	,,	,,	?	S
,,	,,	*Bythoceras*	,,	,,	?	S
,,	,,	*Nassopsis*	,,	,,	?	S
,,	,,	*Paramelania* (Moore, 1898a, 1899b)	,,	,,	?	S
,,	,,	*Paludomus*	,,	,,	?	S
		Melanoides (Seshaiya, 1929a, 1929b)	,,	,,	?	S
,,	Typhobiidae	*Typhobia* (Moore, 1898b)	,,	,,	?	S
,,	Cerithiidae	*Potamides*	Brackish water	,,	?	S
,,	,,	*Potamoides* (Seshaiya, 1932)	,,	,,	?	S
,,	Vermetidae	*Vermetus novae hollandiae* (Yonge, this paper)	Marine	Ciliary	Phytoplankton	RC

TABLE III—*continued*.

Sub-order.	Family.	Genus.	Habitat.	Feeding mechanism.	Food.	Style-sac
Taenioglossa	Turritellidae	*Turritella* (Randles, 1902; Seshaiya, 1932)	Marine	Ciliary[2]	Bottom diatoms, etc.[3]	RC
,,	Aporrhaidae	*Aporrhais* (Digby, 1902)	,,	Radula and sucking proboscis	Ditto[3]	S
,,	Strombidae	*Strombus* (Haller, 1893; Yonge, this paper)	,,	Radula	Algae	S
,,	,,	*Rostellaria* (Haller, 1893)	,,	,,	?	S
,,	,,	*Pterocera* (Huxley, 1853; Woodward, 1894; Yonge, this paper)	,,	,,	Algae	S
,,	Capulidae	*Capulus*	,,	Ciliary	Phytoplankton	RC
,,	,,	*Calyptraea* (Orton, 1922)	,,	,,	,,	RC
,,	,,	*Crepidula* (Orton, 1922; Mackintosh, 1925; Yonge, 1925)	,,	,,	,,	RC
Stenoglossa	..	..	..	..	..	..
Tectibranchia	Limacinidae	*Limacina*, etc.	Marine planktonic	,,	,,	S
,,	Cymbuliidae	*Cymbulia*	Ditto	,,	,,	S
..	..	*Gleba*, etc.	,,	,,	,,	S
,,	Cavoliniidae	*Cavolinia*	,,	,,	,,	S
,,	..	*Creseis*, etc. (Meisenheimer, 1905; Yonge, 1926*d*)	,,	,,	,,	S
Nudibranchia	..	..	..	..	..	..
Order Pulmonata	..	..	..	..	..	..

C = Style-sac in free communication with the intestine.   RC = Style-sac in restricted communication with the intestine.   S = Style-sac separate from the intestine.   [1] Verbal information from Dr. M. V. Lebour.   [2] Personal observations not yet published.   [3] Hunt (1925).

So far as is at present known, the style is restricted to the Rhipidoglossa, Taenioglossa (where alone it is frequently found), and the three families comprising the Thecasomatous Pteropods in the Tectibranchia. The style which has been described in *Patella* (Docoglossa), is actually a firm mucous string. Graham (1932) in recent work on the physiology of digestion in this animal, has shown that there is definitely no evidence of a style. Statements about the presence of a style in *Trochus* are also incorrect. I had the opportunity of examining the very large *T. niloticus* in Australia, and there is no style-sac, style or gastric shield. In view of the morphology of the blind-sac opening into the stomach of the Thecasomatous Pteropods and the nature of the hyaline secretion, there is ample justification for regarding the latter as a crystalline style.

Of the 41 genera listed, 17 are marine, 4 brackish water, 17 freshwater, 2 amphibious

and 1 terrestrial.* Thirty-one of these feed with the aid of a radula and 10 by ciliary mechanisms. In 3 the style-sac is in free communication with the intestine, in 11 in restricted communication, and in 24 it is separate. In 3 cases exact details of the morphology of this region are unknown. In *Paludomus* and *Melanoides*, Seshaiya (1929b) states that the style-sac is united to the intestine for a very short distance about one-tenth of its length. Passing to the food, this consists in all cases where it is known of *vegetable matter*, algae, diatoms and other phytoplankton, freshwater weeds or other vegetation. With one exception the genera for which no data on the food have been found are freshwater. These are almost certainly all herbivorous ; there are apparently *no* carnivorous Gastropoda in fresh water. The food of *Rostellaria* is unknown, but there is every reason for assuming that it is the same as that of its allies in the Strombidae, *Strombus* and *Pterocera*, both of them highly specialized herbivores. It is noteworthy that no indications of a style are present in any of the carnivorous Gastropoda, such as the Heteropods, the Stenoglossa (including such highly specialized carnivores as *Mitra*, *Murex*, *Voluta*, *Oliva*, *Terebra*, and *Conus*, species of all of which are abundant on the Great Barrier Reef, or *Fusus*, *Buccinum*, *Nassa*, *Murex* and *Purpura*, all of which are common round British coasts), or many of the Opisthobranchs.

On the other hand, not all herbivorous Gastropoda possess styles. Such purely herbivorous genera as *Patella* and *Helcion* (Docoglossa), *Haliotis* and *Trochus* (Rhipidoglossa), *Aplysia* and *Dolabella* (Tectibranchia), *Hermaea* and *Caliphylla* (Nudibranchia) and *Helix* (Pulmonata) are all without styles. The presence of this organ is restricted to herbivorous Gastropoda, but is not universal in such animals.

The style is universal in Lamellibranchia, though small, and probably vestigial, in the carnivorous Septibranchia (Yonge, 1928b). With the exception of the Teredinidae and the Septibranchia, two small and specialized groups, feeding is exclusively by ciliary currents. Food is collected comparatively slowly and, when the temperature is above a certain minimum figure, almost continuously. The style, by its rotation, assists alike in the drawing of the food into the stomach and its effective mixing there with the digestive enzymes. In the Lamellibranchia the latter come exclusively from the style itself. This consists of a protein of a globulin nature which is secreted in the style-sac, and on the protein molecules of which the amylase is adsorbed. The style is continually being formed and pushed forward, and as rapidly dissolved away in the stomach owing to the more alkaline reaction of the fluid (Yonge, 1925, 1926c, 1931). The substance of the style is thus the vehicle for the conveyance of the amylase from the site of its secretion to the stomach, where it is liberated. The whole process is one admirably fitted for *the liberation continuously of very small quantities of enzyme*. This, in view of the small but constant stream of food, constitutes a physiological adaptation as efficient as it is unique.

The results of my work on the crystalline style in the Lamellibranchs explain the distribution of this organ amongst the herbivorous Gastropoda. In the first place the Gastropoda with ciliary feeding mechanisms, *Vermetus*, *Turritella*, the Capulidae and the Thecasomatous Pteropods, all possess styles. The other Gastropoda, so far as their feeding habits are known, *e. g.* in the Strombidae, collect their delicate food by the slow but continual rasping action of the radula. Many of the other herbivorous Gastropoda

---

* I have confirmed Garnault's statement that *Pomatias* has a style-sac. It is a very interesting and perhaps significant fact that this organ is found in only one terrestrial genus, and that genus largely subterranean and so probably a more or less continuous feeder.

consume their food at great speed : *Aplysia* can devour a large frond of *Ulva* in a very short time : *Helix* is also a rapid feeder. The crystalline style is confined in the Gastropoda to herbivores which, either by ciliary currents or by a radula, pass a continuous supply of finely-divided food to the stomach. As in the Lamellibranchia, the style assists in the passage of this food through the gut, and provides a vehicle for the continuous discharge of small quantities of amylase into the stomach. The Gastropoda differ from the Lamellibranchia in the presence of other extracellular digestive enzymes, *e. g.* the cellulase in *Pterocera* and *Strombus*, in the stomach in addition to the amylase from the style. These may be secreted in part or entirely by the " salivary " glands, which are absent in the Lamellibranchia.

Robson (1922*b*) has commented admirably on the appearance of the style in both Lamellibranchia and Gastropoda. He notes that these two classes of the Mollusca, very distinct structurally, have " in respect of their digestive system retained in common (*a*) a singularly characteristic structure and (*b*) equal developmental potentiality with regard to it." Wherever the nature of the food and the manner of its collection demands, there a style is found in the Gastropoda. This correlation between food, mode of feeding and structure of the alimentary system is probably best demonstrated in the Thecasomatous Pteropods. These animals descended from carnivorous ancestors, and with the increased specialization of the ciliary feeding mechanisms (adapted for the collection of phytoplankton), there is a progressive reduction in the buccal mass and its associated structures -- radula, jaws and " salivary " glands, all handed down from carnivorous ancestors -- which, though comparatively well developed in *Cavolinia* and *Creseis*, are vestigial in *Cymbulia* and absent in *Gleba* (Yonge, 1926*d*). At the same time a style is acquired.

Both Robson and Mackintosh have drawn particular attention to the different relations which may exist between the style-sac and the intestine in Gastropoda, following up similar observations by Matthias (1914) on the Lamellibranchia. In both Classes there is free communication between the two in the more primitive groups, *e. g.* the Rhipidoglossa and the Protobranchia respectively. In the Lamellibranchia particularly all types of relationships may be found in the more highly organized groups. Matthias suggested, and he is supported by Robson and Mackintosh, that this might be a character of taxonomic significance. In an earlier paper (1923) I gave some support to this view, but further work leads me to believe that these differences may be correlated with the habits of the different animals.

5. SUMMARY.

1. *Pterocera crocata* is abundant on the surface of reefs, usually on the sheltered side and living always in sandy depressions. It is adapted for life on sand.

2. It is exclusively herbivorous, rasping the most delicate algae with its small radula.

3. The anatomy of its digestive system, and particularly of the stomach and of the style-sac, which is separated throughout from the intestine, is described.

4. Owing to its isolation in a separate sac the style is not dissolved when animals are kept out of water for long periods.

5. The ciliary currents in the stomach carry fine particles to the gastric shield and into the ducts of the digestive gland, and convey large particles and indigestible matter to the opening of the intestine.

6. The stomach fluid contains enzymes which rapidly digest starch, glycogen and cellulose, and more slowly sucrose and olive oil. There is *no* protease.

7. The cellulase acts on filter-paper and algae, it has an optimum pH at 5·85 and converts cellulose directly into glucose.

8. Extracts of the style digest starch and glycogen, of the digestive gland starch, glycogen, sucrose and fats but have no action on protein, and of the salivary glands starch and glycogen. The origin of the cellulase could not be determined.

9. Absorption and intracellular digestion probably take place exclusively in the tubules of the digestive gland. The processes of feeding, digestion and assimilation all reveal the high degree of specialization attained by *Pterocera*, and probably all the Strombidae, as herbivores.

10. *Vermetus novae hollandiae* was found only on the outer barrier reefs, where it grows attached to the coral rock. The shell may attain a length of 28 cm. and a width of 3·6 cm.

11. Although the pedal gland secretes a constant stream of mucus, food was never seen to be secured by this means.

12. *V. novae hollandiae* feeds on phyto-plankton, which it secures by ciliary currents on the gills and elsewhere in the mantle cavity, in the same manner as in *Crepidula* and its allies.

13. The alimentary canal is described. There is a crystalline style which lies in a sac in restricted communication with the intestine, and which in consequence rapidly disappears when the animal is in poor condition.

14. The differences between the feeding habits of *V. novae hollandiae* and the Mediterranean species *Vermetus gigas* are such as to demand a reinvestigation of this genus.

15. The differences between species of *Vermetus* which grow on the surface of reefs and of *Magilus* which grow up embedded in living coral are described.

16. The distribution of the crystalline style in the Gastropoda is discussed, and data given about the habitat, feeding mechanisms, food and morphology of the style-sac in the animals which possess this organ.

17. The style is restricted to herbivorous Gastropoda, but is not present in all of these. It is confined to those which feed by ciliary mechanisms, or by the slow but almost continuous action of a radula. It is an organ which assists in the passage of a continuous stream of finely-divided food through the gut, its effective mixing with enzymes in the stomach, and, by its slow dissolution in the stomach, is admirably fitted for the liberation continuously of very small quantities of enzyme.

18. The different relations between the style-sac and intestine are probably correlated with the habits of the particular animals and have no taxonomic significance.

6. REFERENCES.

BOETTGER, C. R. 1930. Studien zur Physiologie der Nahrungsaufnahme festgewachsener Schnecken. Die Ernährung der Wurmschnecke *Vermetus*. Biol. Zbl. L, pp. 581-597.

BOUVIER, E. 1888. Étude sur l'organisation des Ampullaires. Mém. Soc. Phil. Paris, Cent., pp. 63-85, pl. ix.

BOYNTON, L. C., and MILLER, R. C. 1927. The Occurrence of a Cellulase in the Ship-Worm. J. Biol. Chem. LXXV, pp. 613 618.

BREGENZER, A. 1916. Anatomie und Histologie von *Bythinella dunkeri*. Zool. Jahrb. abt. Anat. XXXIX, pp. 237 292, pl. xvi.

COOKE, A. H. 1895. Molluscs. Cambridge Natural History, III, pp. 1 459, text-figs. 1 311.

DIGBY, L. 1902. On the Structure and Affinities of the Tanganyika Gastropods *Chytra* and *Limnotrochus*. Proc. Linn. Soc. Lond. Zool. XXVIII, pp. 434–442, pls. xxxviii–xl.

DORE, W. H., and MILLER, R. C. 1923. The Digestion of Wood by *Teredo navalis*. Univ. Calif. Publ. Zool. XXII, pp. 383–400, pl. xviii.

GARNAULT, P. 1887. Recherches anatomiques et histologiques sur le *Cyclostoma elegans*. Actes Soc. Linn. Bordeaux, XLI, pp. 129–158.

GRAHAM, A. 1931. On the Morphology, Feeding Mechanisms and Digestion of *Ensis siliqua* (Schumacher). Trans. Roy. Soc. Edin. LVI, pp. 725–751, pl. i, text-figs. 1–8.

—— 1932. On the Structure and Function of the Alimentary Canal of the Limpet. Trans. Roy. Soc. Edin. LVII, pp. 287–308, text-figs. 1–10.

HALLER, B. 1888. Die Morphologie der Prosobranchier, gesammelt auf einer Erdumsegelung durch die König. italienische Korvette " Vettor Pisani." Morph. Jahrb. XIV, pp. 54–169, pls. iii–viii.

—— 1893. Die Morphologie der Prosobranchier, gesammelt . . . " Vettor Pisani." Morph. Jahrb. XIX, pp. 553–591, pls. i–iv.

HARINGTON, C. R. 1921. A Note on the Physiology of the Ship-Worm (*Teredo norvegica*). Bio-Chem. J. XV, pp. 736–741, text-fig. 1.

HOUSSAY, F. 1884. Recherches sur l'opercule et les glandes du pied des Gastéropodes. Arch. Zool. Exp. Gén. (2), II, pp. 171–288, pls. vii–xiv.

HUNT, O. D. 1925. The Food of the Bottom Fauna of the Plymouth Fishing Grounds. J. Mar. Biol. Ass. XIII, pp. 560–599, pls. i, ii, text-fig. 1.

HUXLEY, T. H. 1853. On the Morphology of the Cephalous Mollusca. Phil. Trans. Roy. Soc. Lond., B, CXLIII, pp. 29–65.

IHRING, H. VON. 1885. Zur Kenntniss der Gattung Lithoglyphus. Mal. Blätt. VII, pp. 96–99.

KARRER, P., and ILLING, H. 1925. Über die Kinetik des enzymatischen Celluloseabbaues. Helvet. Chim. Acta, VIII, pp. 245–247.

KRIJGSMAN, B. J. 1928. Arbeitsrhythmus der Verdauungsdrüsen bei *Helix pomatia*. II. Teil : Sekretion, Resorption und Phagocytose. Z. vergl. Physiol. (= Abth. C. Z. Wiss. Biol.), VIII, pp. 187–280, pl. i, text-figs. 1–38.

LACAZE-DUTHIERS, H. 1860. Mémoire sur l'anatomie et l'embryologie des Vermets (*Vermetus triqueter et V. semisurrectus* Phil.). Ann. Sci. Nat. (4), Zoologie, XIII, pp. 209–296, pls. iv–ix.

LENSSEN, J. 1899. Système digestif et système génital de la *Neritine fluviatilis*. La Cellule, XVI, pp. 177–232, pls. i–iv.

MACKINTOSH, N. A. 1925. The Crystalline Style in Gastropods. Quart. J. Micr. Sci. LXIX, pp. 317–342, pls. xx, xxi, text-figs. 1–3.

MATTHIAS, M. 1914. Vergleichend-anatomische Untersuchungen über den Darmkanal und das Herz einiger Arcaceen. Jen. Z. Naturw. LII, pp. 363–444, pls. i–iv, text-figs. 1–5.

MEISENHEIMER, J. 1905. Pteropoda. Wiss. Ergebn. Tiefsee Exped. *Valdivia*, 1898–1899, IX, pp. 1–314, pls. i, xxvii, maps i–ix, text-figs. 1–32.

MOORE, J. E. S. 1898a. The Molluscs of the Great African Lakes. I. Distribution. Quart. J. Micr. Sci. XLI, pp. 159–180.

—— 1898b. II. The Anatomy of the Typhobias, with a Description of a New Genus (*Batanalia*). Quart. J. Micr. Sci. XLI, pp. 181–204, pls. xi–xiv.

—— 1899a. III. *Tanganyika rufofilosa*, and the Genus *Spekia*. Quart. J. Micr. Sci. XLII, pp. 155–185, pls. xiv–xix.

—— 1899b. IV. Nassopsis and Bythoceras. Quart. J. Micr. Sci. XLII, pp. 187–201, pls. xx, xxi.

MOQUIN-TANDON, A. 1885. Hist. Moll. France.

NICHOLLS, A. G. 1931. On the Breeding and Growth-rate of the Black-lip Pearl Oyster (*Pinctada margaritifera*). Repts. G. Barrier Reef Comm. Brisbane, III, pp. 26–30, pls. vii, viii.

ORTON, J. H. 1912. The Mode of Feeding in *Crepidula*, with an Account of the Current-producing Mechanism in the Mantle Cavity, and some Remarks on the Mode of Feeding in Gastropods and Lamellibranchs. J. Mar. Biol. Ass. IX, pp. 444–478, text-figs. 1–20.

—— 1922. Occurrence of a Crystalline Style in the American Slipper Limpet (*Crepidula fornicata*) and its Allies. Nature, London, CX, p. 149.

POTTS, F. A. 1923. The Structure and Function of the Liver of *Teredo*, the Shipworm. Proc. Camb. Phil. Soc. (Biol. Sci.) I, pp. 1–17, pls. i, ii, text-figs. 1–5.

RANDLES, W. B. 1902. On the Presence of a Crystalline Style and Style-sac in *Turritella communis*. Anat. Anz. XXI, pp. 200–203, text-figs. 1–3.

ROBSON, G. C. 1921. On the Anatomy and Affinities of *Hypsobia nosophora*. Ann. Mag. Nat. Hist. (9) VIII, pp. 401–413, text-figs. 1–7.

ROBSON, G. C. 1922a. On the Anatomy and Affinities of *Paludestrina ventrosa*. Quart. J. Micr. Sci. LXVI, pp. 159 185, text-figs. 1 12.

—— 1922b. On the Style-sac and Intestine in Gastropoda and Lamellibranchia. Proc. Malac. Soc. Lond. XV, pp. 41 46.

ROUGEMONT. P. de. 1880. Note sur le grand Vermet (*Vermetus gigas* Bivona). Bull. Soc. Sci. Nat. Neuchâtel, XII, pp. 94 97.

SESHAIYA, R. V. 1929a. The Stomach of *Paludomus tanschaurica* (Gmelin). Rec. Ind. Mus. Calcutta, XXXI, pp. 7-12, text-figs. 1 2.

—— 1929b. The Style-sac of some Fresh water Gastropods. Rec. Ind. Mus. Calcutta, XXXI, pp. 101-105, text-figs. 1, 4.

—— 1930. Anatomy of *Mysorella costigera* Kuster. Rec. Ind. Mus. Calcutta, XXXII, pp. 1 28, text-figs. 1 27.

—— 1932. The Style Sacs of some more Gastropods. Rec. Ind. Mus. Calcutta, XXXIV, pp. 171 175, text-figs. 1 4.

SIMROTH, H. 1901a. Gastropoda Prosobranchia. Bronn's Classen und Ordnungen des Tier-Reichs, III.

—— 1901b. Ueber die Ernährung die Tiere und der Weichtiere im besonderen. Verh. 5th Internat. Zoologenkongr. Berlin, pp. 777 785.

WOODWARD, M. F. 1894. On the Anatomy of Pterocera, with some Notes on the Crystalline Style. Proc. Malac. Soc. Lond. I, pp. 143 150, pl. ix.

—— 1899. On the Anatomy of *Adeorbis subcarinatus*. Montague. Proc. Malac. Soc. Lond. III, pp. 140 146, pl. viii.

YONGE, C. M. 1923. The Mechanism of Feeding, Digestion and Assimilation in the Lamellibranch *Mya*. Brit. J. Exp. Biol. I, pp. 15 63, text-figs. 1 27.

—— 1925. The Hydrogen Ion Concentration in the Gut of Certain Lamellibranchs and Gastropods. J. Mar. Biol. Ass. XIII, pp. 938 952.

—— 1926a. The Disappearance of the Crystalline Style. Nature, London, CXVII, p. 691.

—— 1926b. The Digestive Diverticula in the Lamellibranchs. Trans. Roy. Soc. Edin. LIV, pp. 703 718, pls. i, ii.

—— 1926c. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. J. Mar. Biol. Ass. XIV, pp. 295 386, text-figs. 1 42.

—— 1926d. Ciliary Feeding Mechanisms in the Thecasomatous Pteropods. J. Linn. Soc. Lond. Zool. XXXVI, pp. 417 429, text-figs. 1 5.

—— 1928a. Feeding Mechanisms in the Invertebrates. Biol. Reviews. III, pp. 21 76, text-figs. 1 25.

—— 1928b. Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, *Cuspidaria* and *Poromya*. Phil. Trans. Roy. Soc. Lond. B, CCXVI, pp. 221 263, pls. xii xiv, text-figs. 1-7.

—— 1930. The Crystalline Style of the Mollusca and a Carnivorous Habit cannot Normally Co-exist. Nature, London, CXXV, pp. 444 445.

—— 1931. Digestive Processes in Marine Invertebrates and Fishes. J. Con. Intern. Explor. de la Mer, VI, pp. 175 212.

—— 1932a. On the Size Attained by the Crystalline Style in Tridacna and Strombus. Proc. Malac. Soc. Lond. XX, pp. 44 45.

—— 1932b. The Crystalline Style of the Mollusca. Science Progress, XXVI, pp. 643–653, text-figs. 1–6.

Note.—Since this paper was written I have examined several preserved specimens of *Vermetus gigas* obtained from Naples. The gills are very much smaller in proportion than those of *V. novae hollandiae*, and it seems very doubtful whether they could function in the same way. No trace of a style-sac or (more easily determined in preserved material) of a gastric shield was found. There seems little doubt, therefore, that the mode of feeding, food and digestive system in the two species are all totally different. These facts reinforce my statement that further work on the taxonomy of the Vermetidae is essential.